



Network Utility Analysis: A Non-Thermodynamic Constraint to Trophic Transfer Efficiency

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Network utility analysis: a non-thermodynamic constraint to trophic transfer efficiency

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Abstract

The efficiency of resource transfer between trophic levels in an ecosystem tends to be relatively low in spite of the considerable amount of time organisms have had to evolve uptake and assimilation processes. In fact, a general rule of thumb in ecology is that only about 10 percent of the total energy intake into an organism is transferred up to the next trophic level. In addition to the thermodynamic, physical, and chemical limitations, our research indicates another possible limitation to trophic transfer efficiency. Utility analysis, a resource-based input-output measure of the overall usefulness a component's flow has on the entire system, is used to identify the qualitative and quantitative relations in a model. For simple systems, utility is dependent on transfer efficiencies, and in more complex models with feedback and cycling, the relative net transfer efficiency is used. For utility to be calculable, the matrix of direct utility must meet a convergence criterion. However, when these efficiencies are too large this criterion is not met. This is interpreted to mean that utility, which is inherently positive, is not conveyed within these systems. This paper shows, for simple food chain models, where the breakdown in utility analysis occurs and what patterns exist as systems approach this threshold. Although computable utility may not be a necessary condition for low trophic efficiency, it may be sufficient to explain low transfer efficiencies in constituted ecosystems.

Keywords: Network analysis; Utility analysis; Trophic transfer efficiency; Ecological efficiency; Mathematical ecology

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About the Author

This paper was written at the International Institute for Applied Systems Analysis, Laxenburg, Austria, where the author participated in the Young Scientists Summer Program 1997. Brian D. Fath comes from the Institute of Ecology, University of Georgia, Athens, Georgia, 30602, USA.

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Brian D. Fath

1. Introduction

Energy is the ultimate limiting factor to all processes. In a homogenous environment lacking an energy gradient no work can be performed and no life can exist. Life on earth is possible because of the thermal gradient established by the difference between solar (6000 K) and terrestrial (300 K) surfaces. The ecological webs in which organisms are a part capture and concentrate this energy. Once captured this energy establishes the ecosystems "far from equilibrium" and drives them "bottom-up." As the captured energy becomes more concentrated, the exergy of the system increases (Jørgensen, 1994). Living organisms continually work against entropic processes to build and sustain their own life. It has also been proposed that ecosystem development is a response to degrade the energy gradient (Schneider and Kay, 1994). The movement of energy within an ecosystem has been the focus of many studies. Here, input-output utility analysis is used to propose another possible limitation to the efficiency of energy transfer between components of an ecosystem.

There are many physical, chemical, and biological limitations to the effectiveness and efficiency of energy transfer in nature. The laws of thermodynamics provide the first constraints. The first law of thermodynamics states that energy cannot be created or destroyed. Ecologically, this means the sum of all energy that enters into a compartment must equal the sum of all the energy leaving. This law does not implicate the specific form of the energy but rather refers to the energy of all forms passing through the system. Therefore, the efficiency of any energy transfer must range between zero and one hundred percent. The second law of thermodynamics takes into account the form of energy and states that not all the energy in the system can be converted to useful work (exergy). Some energy must be lost as waste heat as the overall entropy of the system increases due to the production and dispersion of 20 low energy infrared photons for every solar photon degraded. Ecologically, this means that not all energy in a compartment can be passed to the next compartment, and the transfer efficiency must be less than one

hundred percent. The second law also requires system openness because compartments are energetically open to their environments.

In addition to thermodynamic constraints to trophic transfer efficiency, there are also ecological constraints. Empirical evidence has shown that trophic transfer efficiencies are relatively low compared to the limit imposed by thermodynamics. "It may be expected that future field estimates [of trophic transfer efficiency] will tend to converge on some relatively narrow range of values around 10 percent" (Slobodkin, 1961, p. 138). This empirical value which is an order of magnitude less than the theoretical limit imposed by thermodynamics may indicate there are other processes limiting the efficiency. One possibility, based on network utility analysis, is investigated in this paper.

2. Methods

2.1. Network analysis

In network ecology, the structure and function of an ecological network is analyzed using mathematical models based on the storages and flows in a system. The techniques used in network ecology originated in input-output economics as a way to identify the relationship between the many sectors of an integrated economic system (Leontief, 1960). Hannon (1973) applied input-output analysis to ecological systems and Finn (1976), Barber (1978), Patten (1978), and Ulanowicz (1986) further extended this methodology. The three main lines of research in network functional analysis are *flow analysis*, *storage analysis*, and *utility analysis*. There is also a structural analysis, *path analysis*, of the associated pathways. Each of the functional analyses is based on a different nondimensional normalization of the flow characteristics of the network. In flow analysis, the flows from component j to

i , f_{ij} , are normalized by the total steady-state throughflow, at component j , $T_j = \sum_{i=0}^n f_{ji} = \sum_{i=0}^n f_{ij}$, where f_{j0}

is the inflow to j from the environment, and f_{0j} is the flow from j to the environment. In storage analysis, the flows are normalized by the steady-state storage at the originating component j (a time step is needed to make this quantity dimensionless). And, in utility analysis, the *net* flow between i and j is normalized by the steady-state throughflow at i . Flow analysis is used to identify system-wide properties of networks such as retention time, turnover rates, cycling rates, and indirect contributions (Hannon, 1973, Finn, 1976, Barber, 1978, Ulanowicz, 1986, Higashi and Patten, 1989). Storage analysis is used in evaluating the stability of the system. Utility analysis is used to identify the direct and indirect qualitative relationships (such as competition, mutualism, etc.) in a network. Utility analysis incorporates the relative net flow between pairs of components and has application to trophic transfer efficiency.

A similar procedure is performed in all three analyses to identify system-wide interactions based on the contributions of all paths of all lengths that arise from the normalized, direct interaction matrices. This procedure takes advantage of the fact that a matrix raised to a particular power gives the influence (expressed nondimensionally) due to all paths of lengths commensurate with the power. Integral interaction matrices are found by summing the infinite power series of the direct interaction matrices. For

example, direct utility is a measure of the net flow matrix normalized by the total throughflow, T_i , at i : $\mathbf{D} = (d_{ij}) = (f_{ij} - f_{ji})/T_i$. The integral utility matrix, \mathbf{U} , which accounts for the contribution of all direct and indirect interactions, is found by summing all powers of \mathbf{D} . \mathbf{U} is an integral utility matrix because its elements represent the total nondimensional utility expressed between the components by powers of \mathbf{D} (Patten, 1991, 1992). The relationships in \mathbf{U} are the basis for the qualitative and quantitative integral utility in the system. The integral flow and storage matrices are similarly derived.

The infinite power series converges when $|\lambda\lambda_m| < 1$, where $\lambda\lambda_m$ is the eigenvalue of the normalized matrix (\mathbf{D} in the case of utility) with the greatest magnitude. The eigenvalues, $\lambda\lambda$, are calculated from the characteristic equation: $|\mathbf{I}\lambda\lambda - \mathbf{D}| = 0$, (Note, when used with matrices $|\cdot|$ means determinant, not absolute value) where \mathbf{I} is the $n \times n$ identity matrix. If $|\lambda\lambda_m| \geq 1$, then the infinite power series does not converge and integral utility is not calculable. When the series converges a general solution can be written in the form:

$$\mathbf{U} = \sum_{k=0}^{\infty} \mathbf{D}^k = (\mathbf{I} - \mathbf{D})^{-1} \quad (1)$$

The convergence criterion is always met for flow analysis because the normalization process ensures openness in the system. The storage analysis can also always be made to converge by choosing an appropriately sized time step. Depending on the flow in the system, it may or may not be met for utility analysis. Integral utility, when calculable, is always positive giving rise to the property network synergism (Fath and Patten, in press). However, nothing can be said about the utility in a system if the power series does not converge. This is interpreted to mean that positive utility is not conferred in these systems.

The integral utility matrix, \mathbf{U} , is an index of the overall relationships in a system. Qualitative interaction types are found by comparing the signs of cross diagonal elements (u_{ij}, u_{ji}) (Patten, 1991). The numerical value gives quantitatively the strength of those interactions. The integral utility matrix, \mathbf{U} , is redimensionalized by multiplying it by $\check{\mathbf{T}}\check{\mathbf{T}}$, where $\check{\cdot}$ means a diagonalized vector. The dimensionalized integral utility matrix is $\mathbf{Y}\mathbf{Y} = \check{\mathbf{T}}\check{\mathbf{T}}\mathbf{U}$. Similarly, the direct utility matrix, \mathbf{D} , can be redimensionalized: $\mathbf{\Delta}\mathbf{\Delta} = \check{\mathbf{T}}\check{\mathbf{T}}\mathbf{D}$. The integral utility values found in $\mathbf{Y}\mathbf{Y}$ are always greater than the direct utility values of $\mathbf{\Delta}\mathbf{\Delta}$. This is network synergism. Since integral utility is more positive than direct utility, this implies that the individual components receive positive utility by being part of the system. The relative strength of the synergism is found by calculating the ratio of positive to negative utility in the system (Eq. (2)).

$$\frac{b}{c} = \frac{\sum \text{utility}_+}{\left| \sum \text{utility}_- \right|} \quad (2)$$

An equivalent test for synergism is to sum the elements of \mathbf{Y} . If the sum is greater than zero, then positive utility is greater than negative utility and network synergism occurs.

2.2. Utilities as transfer efficiencies

The direct utility matrix, \mathbf{D} , can also be derived from the input and output transfer efficiencies in the system. The elements of the output transfer efficiency matrix, \mathbf{G} , give the percent of flow through component j that directly flows to component i , $g_{ij} = f_{ij}/T_j$. The elements of the input transfer efficiency matrix, \mathbf{G}' , give the percent of flow into component i that came directly from component j , $g'_{ij} = f_{ij}/T_i$. Therefore, the direct utility matrix can be written as $\mathbf{D} = \mathbf{G}' - \mathbf{G}^T$ (where \mathbf{G}^T is the transpose of \mathbf{G}). Using this formulation, the direct utility matrix is based on the input and output transfer efficiencies. Eq. (1) can be rewritten such that the integral utility matrix is a function of the transfer efficiencies (Eq. (3)).

$$\mathbf{U} = \sum_{k=0}^{\infty} (\mathbf{G}' - \mathbf{G}^T)^k = (\mathbf{I} - \mathbf{G}' + \mathbf{G}^T)^{-1} \quad (3)$$

The convergence criterion is also a function of the transfer efficiencies. Looking at this problem from another point of view, there is only a certain range of values for the transfer efficiencies for which the convergence criterion is met. If the convergence criterion must be met, then the transfer efficiencies are limited to values in which this occurs. Therefore, the network utility analysis can be used to determine the range of possible values for the transfer efficiencies based on the convergence criterion. Here, we determine the range in which the transfer efficiencies are constrained in order for the utility metric to be calculable and see how this range changes for various structure and flow combinations. In particular, a general pattern regarding the effect of transfer efficiency on utility analysis for food chain models is identified. This analysis is then extended to a complete three component system.

3. Results

3.1. Food Chain

The simplest model in ecology is a food chain. In the unidirectional food chain, all flow comes from the

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & \dots & 0 & 0 \\ f_{21} & 0 & \dots & 0 & 0 \\ 0 & f_{32} & \vdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \dots & f_{n,n-1} & 0 \end{bmatrix} \quad (4)$$

component immediately preceding it ($f_{i,i-1} = T_i$ for $i=2,\dots,n$). Therefore, the value of the elements of \mathbf{G}' are equal to one, and the elements of \mathbf{G} are the output transfer efficiencies along each step of the chain. The integral utility matrix, \mathbf{U} , is calculable when Eq. (1) converges. This occurs when the eigenvalues of

\mathbf{D} are strictly less than one. The characteristic equation associated with $\mathbf{D} = \mathbf{G}' - \mathbf{G}^T$ for a food chain has the following general form:

$$|\mathbf{I}\lambda - \mathbf{D}| = \begin{vmatrix} \lambda & \frac{f_{21}}{T_1} & 0 & 0 & \dots & 0 \\ -\frac{f_{21}}{T_2} & \lambda & \frac{f_{32}}{T_2} & 0 & \dots & 0 \\ 0 & -\frac{f_{32}}{T_3} & \lambda & \frac{f_{43}}{T_3} & \dots & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \frac{f_{n,n-1}}{T_{n-1}} \\ 0 & 0 & 0 & \dots & -\frac{f_{n,n-1}}{T_n} & \lambda \end{vmatrix} = \begin{vmatrix} \lambda & g_{21} & 0 & 0 & \dots & 0 \\ -1 & \lambda & g_{32} & 0 & \dots & 0 \\ 0 & -1 & \lambda & g_{43} & \dots & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & g_{n,n-1} \\ 0 & 0 & 0 & \dots & -1 & \lambda \end{vmatrix} = 0 \quad (5)$$

In a food chain, the convergence test is dependent only on the forward transfer efficiencies. Eq. (5) is a variation of a commonly studied class of matrices called continuants (Muir, 1882, Scott, 1880).

The three component food chain model is ubiquitous in ecology. Slobodkin (1961) introduced a hypothetical model, in which grain flowing down a chute, is eaten by mice as it goes by, and a cat in turn is snatching an occasional mouse, to define ecological efficiency as:

$$\text{Ecological Efficiency} = \frac{\text{calories of mice consumed by cat per unit time}}{\text{calories of grain consumed by mice per unit time}} \quad (6)$$

Ecological efficiency is the ratio of flow from j to i , to the total throughflow at j . This is conceptually and mathematically identical both to g_{ij} in network analysis, and Lindeman efficiency (1942). Therefore, a consistency of terminology exists among the different approaches. Applying Eq. (5) to the three-component food chain, we find that the three eigenvalues associated with the direct utility matrix, \mathbf{D} , are $\lambda = 0, \pm \sqrt{-g_{21} - g_{32}}$. For the convergence test to be met the two transfer efficiencies, g_{21} and g_{32} , their sum must be less than one. Since $0 \leq g_{ij} < 1$, there are cases in which integral utility is not calculable. Network utility analysis places a limitation on the transfer efficiencies of a three-component linear model that the two transfer efficiencies must sum to less than one.

Looking only at cases in which convergence is guaranteed we can investigate how the utility analysis metric is affected by the different transfer efficiencies along each link. Comparing two cases with similar eigenvalues, (determined by $g_{21} + g_{32} = \text{constant}$), shows that b/c is greater for the system in which g_{21} is smaller than g_{12} (Fig. 1). In Fig. 1a $g_{21} = 0.2$ and $g_{32} = 0.7$, whereas in Fig. 1b, $g_{21} = 0.7$ and $g_{32} = 0.2$. In both cases, $\lambda_m = 0.96i$. However, the flows and benefit-to-cost ratios are different. In Fig. 1a, $b/c = 3.88$, and in Fig. 1b, $b/c = 7.91$. Lower g_{21} corresponds to greater energy dissipation from the system in the first step and the energy gradient degrades more rapidly. More generally, we see from Fig.

2 that if $g_{21} = \text{constant}$ and g_{32} increases, then b/c increases slightly; and if $g_{32} = \text{constant}$ and g_{21} increases, then b/c decreases exponentially. If we assume both transfer efficiencies along each link are equal ($g_{21} = g_{32}$) then the individual efficiencies can approach, but not equal 0.50 to meet the convergence criterion. The assumption of equal efficiencies is used later to investigate longer chain models.

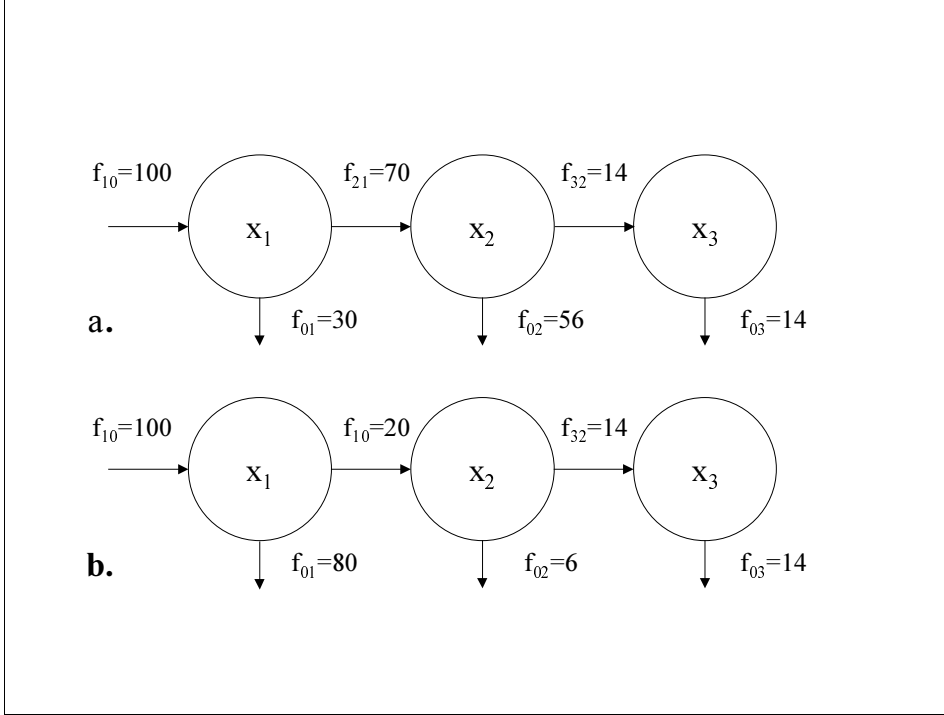


Fig. 1. Comparison of two three-component food chains with different transfer efficiencies

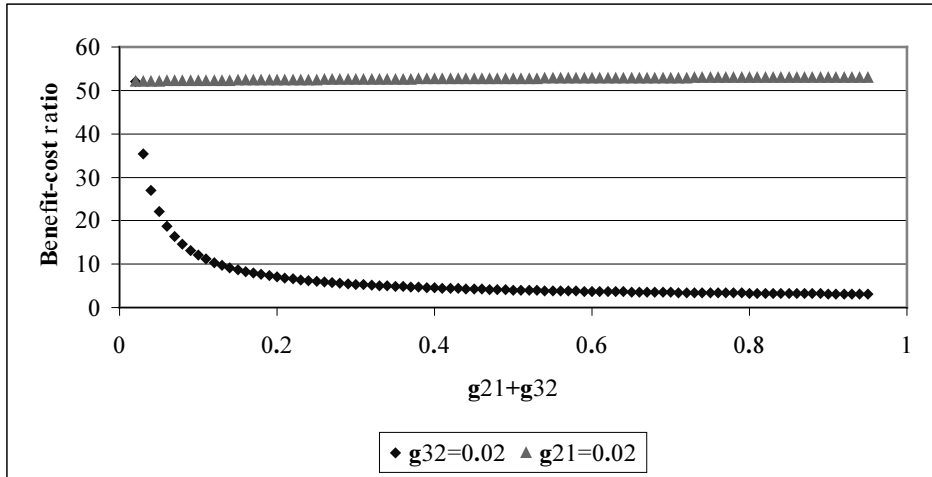


Fig. 2. Effect of changing transfer efficiency on benefit-cost ratio for the three-component food chain. The ratio decreases when g_{21} increase with g_{32} constant. The ratio increases slightly when g_{32} increases with g_{21} constant.

Before leaving the three-component system, we look at another model in which two predators feed on one prey (Fig. 3). In this example, $f_{12} = f_{13} = f_{32} = f_{23} = 0$. The eigenvalues are $\lambda = 0, \pm \sqrt{-g_{21} - g_{31}}$. The total

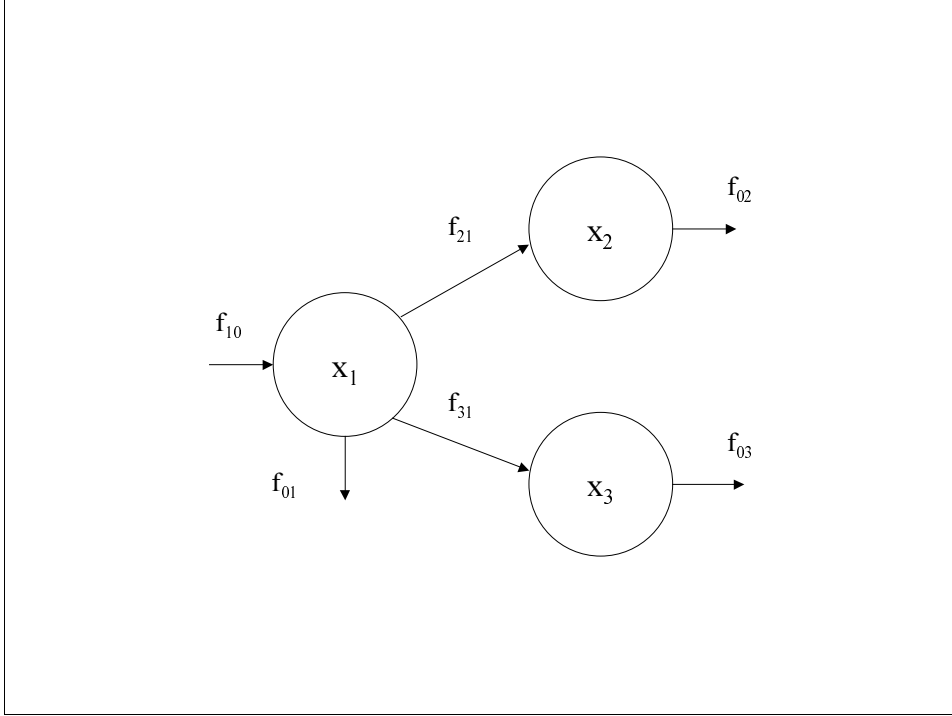


Fig. 3. Three-component competition model.

flow through component x_1 is $T_1 = f_{01} + f_{21} + f_{31}$, and all the transfer efficiencies out of component x_1 sum to unity ($g_{01} + g_{21} + g_{31} = 1$). Since the network is an open, dissipating system, $f_{01} > 0$ and $g_{01} > 0$. Therefore, $g_{21} + g_{31} < 1$ and the convergence test is always met. The integral utility for this model structure is always calculable regardless of the flow through the system. In the three-component food chain, the sum of the two transfer efficiencies, g_{21} and g_{32} , must be less than one for the convergence test to be met and the integral utility calculated. As we increase the number of components in the food chain from three to four, we see that this simple pattern does not continue. The eigenvalues associated with the four-compartment food chain are:

$$\lambda = \pm \frac{\sqrt{2}}{2} \sqrt{-g_{21} - g_{32} - g_{43} + \sqrt{(g_{21} - g_{43})^2 + g_{32}^2 + 2g_{43}g_{32} + 2g_{21}g_{32}}} \quad (7)$$

$$\pm \frac{\sqrt{2}}{2} \sqrt{-g_{21} - g_{32} - g_{43} - \sqrt{(g_{21} - g_{43})^2 + g_{32}^2 + 2g_{43}g_{32} + 2g_{21}g_{32}}}$$

The role of the transfer efficiencies in determining the eigenvalues is still present, but has become algebraically more complicated. The convergence criterion is no longer dependent solely on the sum of the individual transfer efficiencies, but on the sum plus several higher order interaction terms. To observe

a pattern of convergence, we again assume that the transfer efficiencies along each link of the food chain are equal ($g_{ij}=x$, where $0 \leq x < 1$). The eigenvalues for an n -component food chain of this form are derived from the general form:

$$|\mathbf{I}\lambda - \mathbf{D}| = \begin{vmatrix} \lambda & x & 0 & 0 & \dots & 0 \\ -1 & \lambda & x & 0 & \dots & 0 \\ 0 & -1 & \lambda & x & \dots & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & \ddots & \ddots & x \\ 0 & 0 & 0 & \dots & -1 & \lambda \end{vmatrix} = 0. \quad (8)$$

If P_n is the polynomial for an n th order food chain we can write a general expression for P_n as:

$$P_n = \lambda |P_{n-1}| + x |P_{n-2}|. \quad (9)$$

Since we are interested in cases when $|\lambda| < 1$, the greatest value for x , corresponding to the largest possible **transfer efficiency**, will **occur at the limit** as $|\lambda| \rightarrow 1$. As stated earlier, the nonzero eigenvalues of \mathbf{D} are always imaginary. If we let $\lambda \rightarrow 1$ in Eq. (9), then all roots of the polynomial are negative. Therefore, we are only interested in the modulus of x , not the sign. Clearly, x must always be positive because it is the transfer efficiency or transfer probability. Positive roots (with the same value) of the polynomials can be obtained by changing the sign of the recursion relation so that we get

$$P_n = |P_{n-1}| - x |P_{n-2}|. \quad (10)$$

A closed form solution to the recurrence relation in Eq. (11) is given by (See Appendix):

$$P_n(x) = \frac{(1 + \sqrt{1-4x})^{n+1} - (1 - \sqrt{1-4x})^{n+1}}{2^{n+1} \sqrt{1-4x}}. \quad (11)$$

Eq. (12) is used to generate the polynomial equation for any n component food chain. The first seven polynomials are:

$$\begin{aligned}
P_0 &= && +1 \\
P_1 &= && +1 \\
P_2 &= && -x & +1 \\
P_3 &= && -2x & +1 \\
P_4 &= & +x^2 & -3x & +1 \\
P_5 &= & +3x^2 & -4x & +1 \\
P_6 &= & -x^3 & +6x^2 & -5x & +1
\end{aligned} \tag{12}$$

An n th order polynomial has n roots, however, it is the smallest root, r_{\min} , which ensures that $|\lambda\lambda_m| < 1$. The smallest roots form an upper bound on the maximum transfer efficiencies admissible that will allow calculation of integral utilities. If we continue this series of polynomials, it would become evident that the coefficients of the polynomials are equivalent to those found along the diagonals in Pascal's triangle. The right most column are the x^0 terms and the columns moving to the left represent higher powers of x (Eq. 14). (Note also that the sum of the coefficients for P_n gives the Fibonacci number, F_n , where $F_n = F_{n-1} + F_{n-2}$).

Pascal's Triangle =

$$\begin{array}{cccccccc}
& & & & & & & 1 \\
& & & & & & 1 & 1 \\
& & & & & 1 & 2 & 1 \\
& & & & 1 & 3 & 3 & 1 \\
& & & 1 & 4 & 6 & 4 & 1 \\
& & 1 & 5 & 10 & 10 & 5 & 1 \\
& 1 & 6 & 15 & 20 & 15 & 6 & 1 \\
1 & 7 & 21 & 35 & 35 & 21 & 7 & 1
\end{array} \tag{13}$$

$$\begin{array}{cccccccc}
-x^7 & x^6 & -x^5 & x^4 & -x^3 & x^2 & -x^1 & x^0
\end{array}$$

Using Pascal's triangle to get the coefficients for P_n , we numerically find the roots associated with different size food chains. As the number of components in the chain increases, the smallest root of the equation asymptotically approaches 0.25 (Fig. 4) (See Appendix). Fig. 4 shows the largest possible transfer efficiency value for an n component food chain with equal transfer along each $n-1$ links. The

efficiency values are constrained to lie within the area below this curve. The integral utility of a chain of any length is calculable provided the transfer efficiencies are below 0.25 in value.

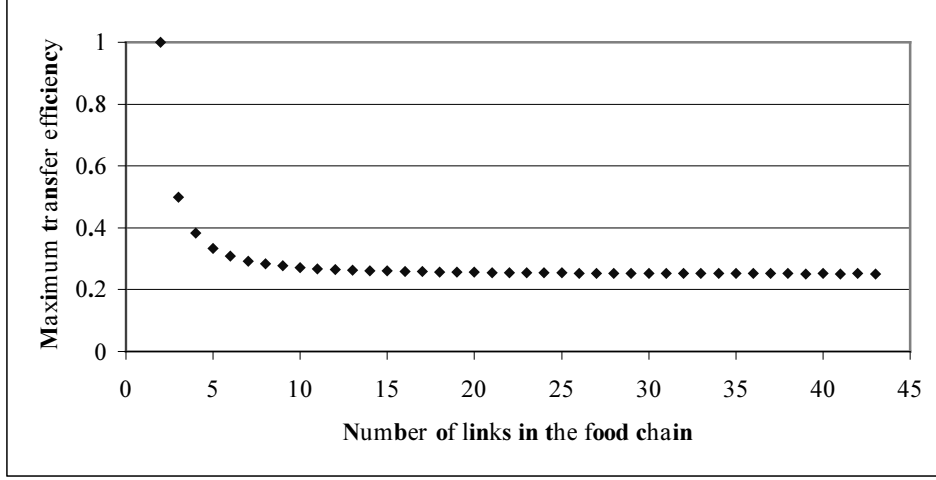


Fig. 4. Maximum transfer efficiency for a food chain with equal transfer efficiencies

3.2. Three component complete system

If we relax the assumption that the system must be a chain, we get a general expression for the characteristic equation for the complete three-component system (Fig. 5):

$$\lambda \left(\lambda^2 + \frac{(f_{12} - f_{21})^2}{T_1 T_2} + \frac{(f_{13} - f_{31})^2}{T_1 T_3} + \frac{(f_{23} - f_{32})^2}{T_2 T_3} \right) = 0 \quad (14)$$

Written in terms of the input and output transfer efficiencies, g_{ij} and g'_{ij} , the characteristic equation is:

$$\lambda \left(\lambda^2 + (g_{12} g'_{12} - 2 g_{12} g_{21} + g_{21} g'_{21}) + (g_{13} g'_{13} - 2 g_{13} g_{31} + g_{31} g'_{31}) + (g_{23} g'_{23} - 2 g_{23} g_{32} + g_{32} g'_{32}) \right) = 0 \quad (15)$$

Now, the eigenvalues of the \mathbf{D} matrix depend not only on the output transfer efficiencies, \mathbf{G} but also on the input efficiencies, \mathbf{G}' . Solving for the eigenvalues back in terms of the flows gives:

$$\lambda = 0, \pm \sqrt{-\frac{(f_{12} - f_{21})^2}{T_1 T_2} - \frac{(f_{13} - f_{31})^2}{T_1 T_3} - \frac{(f_{23} - f_{32})^2}{T_2 T_3}} \quad (16)$$

For this model, the systems which do not meet the convergence criterion (i.e. $|\lambda| > 1$) have a large net flow exchange between compartments. This can be minimized by either low transfer efficiencies or by even flow of energy.

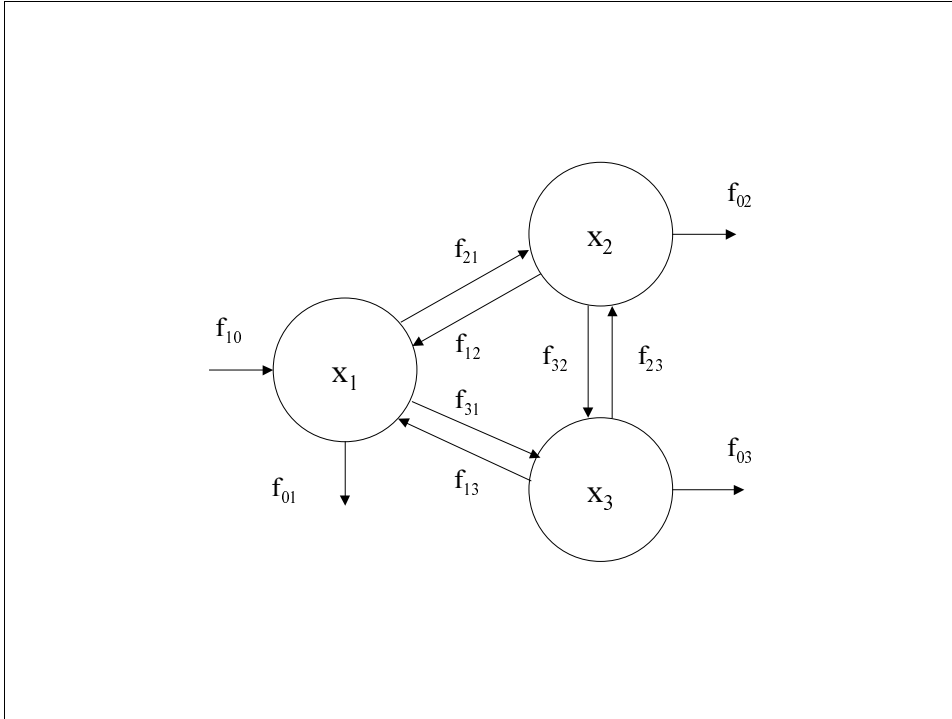


Fig. 5. Three-component complete digraph

3.3. Empirical evidence

The theoretical limit to transfer efficiency based on the utility analysis measure states that the trophic transfer efficiency of a food chain must decrease as the number of components in the chain increases. In an earlier work Patten (1959) compared the flow of energy and transfer efficiencies in four classic ecosystem projects: Lake Mendota (Juday, 1940), Cedar Bog Lake (Lindeman, 1942), Root Spring (Teal, 1957), and Silver Springs (Odum, 1957) (Table 1). The efficiency is calculated by dividing the flow to the n th trophic level by the flow to the previous trophic level. He found that in general the ecological efficiency within the systems ranged between 5 and 20 percent. The one exception, flow to herbivores in the Root Spring system, occurs because there is a large supply of allochthonous input, making the efficiency appear greater when in fact much of the energy into the herbivore compartment did not pass through the producer compartment.

Table 1. Production is expressed in terms of g-cal / cm² / year

Flow to	Lake Mendota (Juday, 1940)	Cedar Bog Lake (Lindeman, 1942)	Root Spring (Teal, 1957)	Silver Springs (Odum, 1957)
Producers	480.0	111.3	306.0	2129.6
Herbivores	42.0	14.8	231.8	336.8
Carnivores	2.3	3.1	20.8	38.3
Top Carnivores	0.3	0.0	0.0	2.1
Flow efficiency to (percent)				
Herbivores	8.8	13.3	75.8	15.8
Carnivores	5.5	20.9	9.0	11.4
Top Carnivores	13.0	0.0	0.0	5.5

4. Conclusions

Network utility analysis has been used to investigate limitations to trophic transfer efficiency. The integral utility metric, when calculable, is always positive giving rise to the property of network synergism. It is not calculable when the eigenvalues of the system are too large, and in a food chain the eigenvalues are dependent solely on the transfer efficiencies. By setting the transfer across each link equal we see that a general pattern emerges. In particular, we have found that in short chains tradeoffs between the various efficiencies are important-if one goes up others must come down. For a three-component system a chain with greater dissipation along the first path has a higher b/c ratio (greater utility). This is unexpected if we assume the system is trying to maximize its efficiency. It contrasts with the generally held concepts that as an ecosystem develops the maximum power (Lotka, 1922) and maximum efficiency (Odum, 1969) of the system increases. However, it may fit well with the maximum exergy degradation principle which states that "as ecosystems grow and develop, they should increase their total dissipation by developing structures and processes to assist energy degradation" (Schneider and Kay, 1994).

Once a chain is longer than three components, the overall efficiency is not a sum of parts. The eigenvalues are more complexly dependent on the transfer efficiencies. Since the efficiency value for the n component chain asymptotically approaches 0.25 as $n \rightarrow \infty$, there is no theoretical limit to the number of components in an isolated food chain. The efficiency never drops to zero. If it did, this would indicate that there is a theoretical limit to the number of components because it is impossible to add another

component if the efficiency to get there is zero. This also implies that adding another compartment has less influence on the previous ones as the number of components increases.

The transfer of energy within an ecosystem is constrained by many processes. Thermodynamically, the cumulative efficiency must be between zero and one. However, empirical results (Slobodkin, 1961, Patten, 1959) indicate that the transfer efficiency is generally considerably less than the theoretical limit imposed by thermodynamics. This paper shows, using network analysis and food chain models, that in cases in which transfer efficiencies are high the convergence criterion is not met. In order for the integral utility to be calculable efficiencies must be relatively low, and therefore it may also be true that transfer efficiencies observed in nature have to be low for the system to receive systemic benefits. This is a system design criterion not inherent in other aspects (physicochemical) of ecosystem energetics. Network utility analysis is relatively a new way of viewing the interactions and relationships between components in a connected system and much work is still needed to understand the nuances and subtleties of this approach.

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Appendix

We want to find a closed form solution to the recurrence relation in Eq. (10) in the text:

$$P_{n+2} = |P_{n+1}| - x |P_n| \quad (\text{A17})$$

Rewriting Eq (10) using a z transformation gives:

$$z^2 P(z) - z^2 \sum_{k=0}^1 z^{-k} = z^1 P(z) - z^1 \sum_{k=0}^1 P_k z^{-k} - x P(z) \quad (\text{A18})$$

and then simplifying

$$z^2 P(z) - z^2 (P_0 + P_1 z^{-1}) = z P(z) - z P_0 - x P(z) \quad (\text{A19})$$

$$z^2 P(z) - z^2 P_0 - z^1 P_1 = z P(z) - z P_0 - x P(z) \quad (\text{A20})$$

$$P(z) (z^2 - z + x) = z^2 P_0 + z P_1 - z P_0 \quad (\text{A21})$$

$$P(z) = \frac{z^2 P_0 + z P_1 - z P_0}{z^2 - z + x} \quad (\text{A22})$$

$P(z)$ is the tranformation of $P(x)$. Given the initial conditions,

$$P_0 = P_1 = 1 \quad (\text{A23})$$

we get:

$$P(z) = \frac{z^2}{z^2 - z + x} \quad (\text{A24})$$

Now, transform back to the x domain using the inverse transform:

$$P_n(x) = \frac{1}{2\pi i} \int \frac{z^2 z^{n-1}}{z^2 - z + x} dz \quad (\text{A25})$$

$$P_n(x) = \frac{1}{2\pi i} \int \frac{z^{n+1}}{z^2 - z + x} dz \quad (\text{A26})$$

The roots of $z^2 - z + x$ are:

$$\begin{aligned}\lambda_1 &= \frac{1 + \sqrt{1-4x}}{2} \\ \lambda_2 &= \frac{1 - \sqrt{1-4x}}{2}\end{aligned}\tag{A27}$$

$$P_n(x) = \frac{1}{2\pi i} \int \frac{z^{n+1}}{z^2 - z + x} dz = \text{Residue}(\lambda_1) + \text{Residue}(\lambda_2)\tag{A28}$$

$$\text{Residue at } \lambda_1: \left. \frac{z^{n+1}}{z - \lambda_2} \right|_{z=\lambda_1} = \frac{\lambda_1^{n+1}}{\lambda_1 - \lambda_2}\tag{A29}$$

$$\text{Residue at } \lambda_2: \left. \frac{z^{n+1}}{z - \lambda_1} \right|_{z=\lambda_2} = \frac{\lambda_2^{n+1}}{\lambda_2 - \lambda_1}\tag{A30}$$

$$P_n(x) = \frac{\lambda_1^{n+1} - \lambda_2^{n+1}}{\lambda_1 - \lambda_2}\tag{A31}$$

$$\lambda_1 - \lambda_2 = \sqrt{1-4x}\tag{A32}$$

Eq (A33) gives one form for $P_n(x)$:

$$P_n(x) = \frac{(1 + \sqrt{1-4x})^{n+1} - (1 - \sqrt{1-4x})^{n+1}}{2^{n+1} \sqrt{1-4x}}\tag{A33}$$

This is the form of Eq. (11) in the text. It can be rewritten to see more clearly the relation between x and

n . Looking at the numerator first, we let $b = \sqrt{1-4x}$ and expand using the binomial theorem

$$(1+b)^{n+1} = \sum_{i=0}^{n+1} \binom{n+1}{i} b^i 1^{n+1-i}\tag{A34}$$

$$(1-b)^{n+1} = \sum_{i=0}^{n+1} \binom{n+1}{i} b^i (-1)^i\tag{A35}$$

$$(1+b)^{n+1} - (1-b)^{n+1} = \sum_{i=0}^{n+1} \binom{n+1}{i} b^i (1-(-1)^i) \quad (\text{A36})$$

$$(1+b)^{n+1} - (1-b)^{n+1} = \sum_{i=0}^{\left\lfloor \frac{n}{2} \right\rfloor} \binom{n+1}{2i} b^{2i} (1-(-1)^{2i}) + \sum_{i=0}^{\left\lfloor \frac{n}{2} \right\rfloor} \binom{n+1}{2i+1} b^{2i+1} (1-(-1)^{2i+1}) \quad (\text{A37})$$

The first summation includes the even terms, and the second, the odd terms. However, all the even terms are zero because $1-(-1)^{2i}$ is zero. Therefore all we are left with is:

$$(1+b)^{n+1} - (1-b)^{n+1} = \sum_{i=0}^{\left\lfloor \frac{n}{2} \right\rfloor} \binom{n+1}{2i+1} b^{2i+1} (1-(-1)) \quad (\text{A38})$$

Substituting back in for b gives:

$$(1+\sqrt{1-4x})^{n+1} - (1-\sqrt{1-4x})^{n+1} = 2 \sum_{i=0}^{\left\lfloor \frac{n}{2} \right\rfloor} \binom{n+1}{2i+1} (\sqrt{1-4x})^{2i+1} \quad (\text{A39})$$

Substituting this back in for $P_n(x)$ gives:

$$P_n(x) = \frac{2}{2^{n+1} \sqrt{1-4x}} \sum_{i=0}^{\left\lfloor \frac{n}{2} \right\rfloor} \binom{n+1}{2i+1} (\sqrt{1-4x})^{2i+1} \quad (\text{A40})$$

Eq. (A41) gives a second form for $P_n(x)$:

$$P_n(x) = \frac{1}{2^n} \sum_{i=0}^{\left\lfloor \frac{n}{2} \right\rfloor} \binom{n+1}{2i+1} (1-4x)^i \quad (\text{A41})$$

Using Eq. (A41), we see that around the point $x=1/4$, the higher order terms of i become negligible. So solving $P_n(x)$ looking at only the terms when $i=0$ and $i=1$ we get:

$$P_n(x) = \frac{1}{2^n} \left[n+1 + \binom{n+1}{3} (1-4x) \right] \quad (\text{A42})$$

Since we are looking for the root we set Eq (A42) equal to zero and solve for x .

$$n+1 + \frac{(n+1)n(n-1)(n-2)!}{3!(n-2)!}(1-4x)=0 \quad (\text{A43})$$

$$n+1 + \frac{(n+1)n(n-1)}{6}(1-4x)=0 \quad (\text{A44})$$

$$n(n-1)(1-4x)=-6 \quad (\text{A45})$$

$$x = \frac{1}{4} + \frac{3}{2n(n-1)} \quad (\text{A46})$$

Now, it is clear that as $n \rightarrow \infty$, $x \rightarrow 1/4$.